

INVITED REVIEW

Putting the Plants Back into Plant Ecology: Six Pragmatic Models for Understanding and Conserving Plant Diversity

PAUL KEDDY*

*Schlieder Endowed Chair for Environmental Studies, Southeastern Louisiana University,
Hammond, LA 70402, USA*

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• *Background* There is a compelling need to protect natural plant communities and restore them in degraded landscapes. Activities must be guided by sound scientific principles, practical conservation tools, and clear priorities. With perhaps one-third of the world's flora facing extinction, scientists and conservation managers will need to work rapidly and collaboratively, recognizing each other's strengths and limitations. As a guide to assist managers in maintaining plant diversity, six pragmatic models are introduced that are already available. Although theoretical models continue to receive far more space and headlines in scientific journals, more managers need to understand that pragmatic, rather than theoretical, models have the most promise for yielding results that can be applied immediately to plant communities.

• *Six Pragmatic Models* For each model, key citations and an array of examples are provided, with particular emphasis on wetlands, since 'wet and wild' was my assigned theme for the Botanical Society of America in 2003. My own work may seem rather prominent, but the application and refinement of these models has been a theme for me and my many students over decades. The following models are reviewed: (1) species–area: larger areas usually contain more species; (2) species–biomass: plant diversity is maximized at intermediate levels of biomass; (3) centrifugal organization: multiple intersecting environmental gradients maintain regional landscape biodiversity; (4) species–frequency: a few species are frequent while most are infrequent; (5) competitive hierarchies: in the absence of constraints, large canopy-forming species dominate patches of landscape, reducing biological diversity; and (6) intermediate disturbance: perturbations such as water level fluctuations, fire and grazing are essential for maintaining plant diversity.

• *Conclusions* The good news is that managers faced with protecting or restoring landscapes already have this arsenal of tools at their disposal. The bad news is that far too few of these models are appreciated.

Key words: Competition, conservation, disturbance, diversity, gradients, herbaceous vegetation, management, pragmatic approaches to ecology, pragmatic models, rare plants, richness, theoretical models.

PART I. PRAGMATIC AND THEORETICAL MODELS: ESSENTIAL DIFFERENCES

Ecological models are a valuable tool for synthesis. Models may show how widely different vegetation types containing plants with different evolutionary origins may still be controlled by the same few organizing principles and ecological factors. There are at least two classes of models available now (Fig. 1). One class (extensively covered in major journals; Fig. 1A) is the product of theoreticians; the other (less well-appreciated, Fig. 1B) is the product of empiricists and pragmatists. These distinctions may seem somewhat arbitrary, but they highlight fundamentally different attitudes toward plant ecology, to science in general and to botany in particular.

Pragmatists tend to believe that the way to build a body of general principles is to start small with models that concisely describe observed patterns in pieces of reality. One then patiently seeks to connect these models into a larger whole. Over the past 20 years, plant ecologists have accumulated the set of such models introduced here. This list could easily be extended by adding even more basic models of bivariate relationships such as species latitude patterns (Gaston, 2000) or the regression relationships linking plankton production to N and P concentration in lakes

(Smith, 1982). Some might argue that a regression line is not a 'model.' I disagree, but then I am more of a pragmatist. If one is willing to accept other abstractions that summarize relationships in the Earth's biota, we might even consider descriptive maps such as world floristic regions (Takhtajan, 1969, 1986) or diversity hot-spots (Myers *et al.*, 2000) to be pragmatic models.

There has been modest progress with each of the six models described in Part II (species–area, species–biomass, centrifugal organization, species–frequency, competitive hierarchies and intermediate disturbance). Consider Grime's 'humped-back' species–biomass model. First published in 1973 to describe how diversity first increases and then decreases with biomass in English grasslands (Grime, 1973a), it was extended to a broader array of English upland vegetation types in the 1970s (Grime, 1973b, 1979). It was then tested and found to apply in other habitat types such as wetlands and Mediterranean grasslands. The model is now generally accepted and applied worldwide to manage vegetation to enhance local diversity.

For pragmatists, the pattern comes first, and the mechanisms come later. The logic is this: it is worth doing the difficult and time-consuming experimental work to unravel mechanisms only if there is a pattern in the first place. Field experiments of competition are now unravelling the complicated relationships among competition, stress and

* For correspondence. E-mail pkeddy@selu.edu

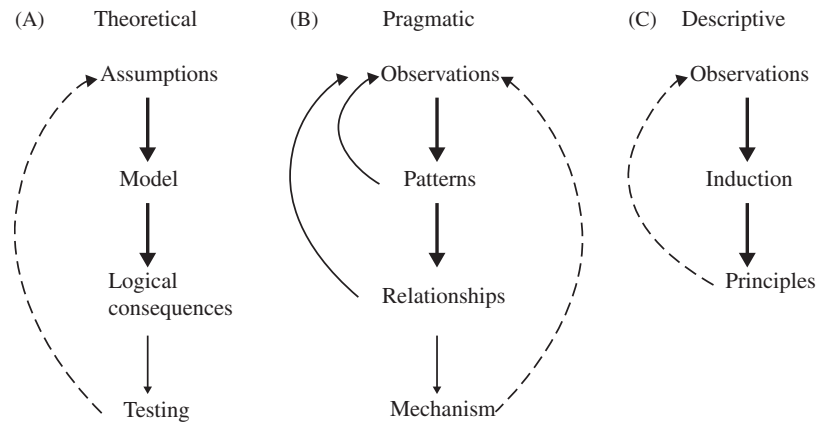


FIG. 1. Three approaches to plant ecology. The two extremes are theoretical models (A) and collections of data (C). The pragmatic approach (B) offers a middle approach. Theoretical models explore only the logical consequence of assumptions—the difficulty in testing both the assumptions and outcomes (dashed line) is the weak link. Descriptive studies can lead to endless data collection and rely upon induction to find general principles in these data—but, as with theoretical models, the principles can be tested by collecting new observations. In pragmatism, there is more interplay between observations and patterns. Mechanisms are explored only once general relationships confirm that the patterns are worthy of further exploration.

disturbance that create the deceptively simple ‘humped-back’ pattern (Keddy, 2001).

Some scientists are intolerant of this patient and plant-oriented process of developing and testing models, and, by nature, seem to be less impressed with utility as a criterion of value. They prefer the grand scope of all-encompassing theoretical models. One starts with a few postulates, and then builds a large mathematical model to explore the logical consequences of the postulates (Yodzis, 1989). Theoreticians (*sensu strictu*), then, are primarily interested in following the logical consequences of their assumptions. Their models provide a broad picture of how plant communities might be organized and how they might function were they to correspond to the assumptions that are made. Often it is assumed that other individuals will then do the hard and messy work of testing and applying the model. Because the assumptions in the model might include how plants forage, or compete, or respond to herbivores, such models can be called ‘mechanistic.’ From the perspective of theoreticians, pragmatic models appear to do little more than peddle phenomenology—the collection of facts without a theoretical framework to justify them.

Theoretical ecology, like any scientific culture, has its weaknesses. Anyone who plays video games knows the inherent preference for ever larger games with ever more special effects that run on ever more powerful computers. Theoreticians naturally seem to come from this culture. Indeed, plant ecology is perhaps now experiencing the consequences of an invasion by mathematicians and physicists (e.g. May, Levin, Yodzis) as well as their acolytes (e.g. Tilman, Pacala, Crawley, Loreau). Count how many now appear, sometimes in tandem, on the editorial boards of prominent journals, and also note how densely they cite each others studies. This may partly explain why we are seeing enormous numbers of papers with untestable models in our leading journals, even though these papers ignore important earlier work and make wildly unrealistic assumptions about plants. In contrast, some theoreticians appreciated living organisms—MacArthur knew his warblers, and

Pielou knew her plants. There may now be a critical mass of pseudo plant ecologists who prefer the stark simplicity of mathematical models (constructed in the safety of an air-conditioned or heated office) to the dirty reality of wading through swamps, hiking through forests, climbing tepuis (high-elevation rock outcrops that are insular habitats in forested landscapes), and sweating in outdoor experiments to work with real plants and real plant communities. In my personal experience, some of these prolific writers do not even recognize the names of common (let alone rare) plants or even the names of classic botanists. Relative to the slow and patient attitudes absolutely required for field botany and outdoor experiments, it is now easy, perhaps too easy, to generate large models with complex structures that are extremely difficult (or even impossible) to test. Without tests to determine whether the model usefully describes reality, theoretical models, like outdated video games, tend to accumulate. Too many theoretical models are not falsifiable, and, when data on real plants are carefully gathered to test the models, theoreticians try to trash the data rather than admit the failure of the model. As but one example, note how *The American Naturalist* allowed a theoretician not one, but two opportunities in print (Tilman, 1991a, b) to attack the quality of a data set painstakingly collected on 68 wetland plant species (Shipley and Peters, 1990) to test one of his models. Sixty-eight species is a large data set, and there is no space here, and no editor yet brave enough, to permit me to document all the evasions, botanical falsehoods and failed referencing found in these two so-called rebuttals of the Shipley and Peters data. Clearly the model was more important than the botanical reality—and not just to the author, but to the editors of the journal as well, since one presumes that they reviewed these two rebuttals and hand-picked the referees.

Without falsifiability, i.e. without admitting that a model might be shown to be incorrect (using real data from real plants), other criteria emerge as pseudo-scientific, pseudo indicators of scientific value—criteria such as the complexity of the model, or the size of the computer used to run it.

Falsifiability is never easy. Each model produces output, usually a pattern. There is an unfortunate and entirely mistaken tendency to assume that if a model generates a recognizable pattern, then both the assumptions and the mathematical structure of the model are ‘correct.’ Of course, there are two errors in this thinking: (1) many logically contradictory models can yield similar patterns; and (2) most models generate patterns that are already well documented. If a model merely reproduces a well-known result (e.g. big plants shade out small ones), it can hardly be argued that the model has advanced science. But since the results (the patterns) are broadly known in advance this encourages (even requires that) theoreticians construct models that show the obvious. If a model yielded unrealistic or unexpected patterns it might be considered a failure (even though it could be useful by showing that one set of assumptions is wrong). Pragmatic models, by their very nature, tend to sidestep such problems. There are several reasons for this. Partly it is because they start with real data instead of assumptions. Partly it is because the pragmatic process outlined in Fig. 1 requires continual revision of the model in light of newly accumulated data. Partly it is because the issue of mechanism need not be addressed until rather later in the process. Overall, testing and verification are part of the process from the start. This also means that false models are rapidly detected and rarely develop a life of their own.

In apparent contradiction with the need to show the obvious, novelty is also highly regarded. The easiest way to achieve novelty is to pretend that the patterns, or the assumptions, or both, are new. Of course, novelty may be a valuable quality in any realm of science—I refer here only to the sense of novelty for novelty’s sake rather than genuine new views of reality. One easy way to obtain novelty is to ignore preceding work. Who can build a career publishing models that say, ‘I have made assumptions that everyone knows to be true and found patterns that are already well documented in the literature’?

Perhaps one reason for the foregoing problems is that some theoreticians have almost no interest in plants—even if their work is published in ecological journals, and even if it allegedly involves living organisms. Recall Hutchinson’s famous paper ‘Homage to Santa Rosalia’ (in *The American Naturalist*) (Hutchinson, 1959) where he says up front (at least he was honest) that his objective was to explore biological diversity without having to make the effort to consider plants. ‘[W]hy are there so many kinds of plants? As a zoologist I do not want to ask that question directly. I want to stick with animals but also get the answer’. It can be seen implicitly in work like Lord Robert May’s paper in *Science* ‘How many species are there on Earth?’ where there is but one (unreferenced!) mention of plants and fungi (May, 1988). I have described elsewhere (Keddy, 2005) how this may be the consequence of a generation of scientists raised with papers such as those of Hutchinson (1959) and May (1988), not to mention text books such as those of Hazen (1970) and Strong *et al.* (1984), all of which implicitly and explicitly ignore actual data from real plant communities.

Overall, then, theoreticians are under pressure to produce large and very general models that produce obvious results

and ignore the previous work in the field. Let it be clear that I appreciate theoretical work—but only when it is testable, or at least respectful of the complexities of living organisms and the contingencies of natural systems. Another way of expressing this might be that modelling should have a certain modesty about it: Pielou (1977), Yodzis (1989) and Starfield and Bleloch (1986) have all written about the value of the simplification provided by mathematical models—but all emphasize in their own way the need (using Yodzis’s words) to ‘strike that right balance between detail and generality, between thoroughness and workability’ (p. 3).

Instead of striving modestly for such balance, the recent literature in plant ecology suggests that we have been borrowing attitudes from, and even hiring from, the pretentious realm of theoretical physics. I will leave it for someone else to write an essay about the pretension of theories that promise to explain ‘everything’ as if they can account for, say, the distribution of dark matter in the cosmos and also tell us who wrote *The Epic of Gilgamesh*, whether the Shroud of Turin is real, how *Lachnanthes caroliniana* dispersed from the Pine Barrens of New Jersey to Ponhook Lake in Nova Scotia, as well as perhaps where I lost my car keys while cross-country skiing in 1977. Do I seem to exaggerate? In one recent example, *Ecology* published 16 pages (and a front cover figure) in which Naeem (2002) [simultaneously ignoring relevant treatises such as Ehrlich and Ehrlich (1981) or de Groot (1992)], applauds Tilman, himself and Loreau (citing eight, ten and four of their papers, respectively) upon ‘the emergence of a new paradigm, one in a series of debates associated with the dialectic that has structured ecological inquiry over two millennia of Western science’ (p. 1537). Another case is described in (Keddy, 2005).

Of course, my complaint is hardly original. Swift, who lived around the time of Bacon and Descartes, wrote ‘A Voyage to Balnibarbi’ (in *Gulliver’s Travels*; Swift, 1726), in which he mocked scientists in the grand academy of Lagado for their ambitions—proposing to extract sunbeams from cucumbers or convert excrement back to food. One ingenious architect, he says, proposed to build houses beginning with the roof and working downwards to the foundation (today might that architect become a theoretical ecologist?). Swift comments, too, upon scientific avarice, noting ‘their practice of begging from all who go to see them’ (p. 107). Nearly 2000 years before Swift, in *The Clouds*, the Greek playwright Aristophanes made fun of scholarly debate, right down to offering a false dichotomy—the issue of whether gnats produce their hum by way of their mouth or their anus.

Theoreticians, of course, can respond in kind. Too much current plant ecology may indeed be phenomenology. One could argue, for example, that nearly any experiment employing fertilization or the removal of neighbours will produce some results, and therefore will be publishable (somewhere), whether the data advance the cause of science or not. Facts without some theoretical context may indeed be relatively useless. In the field of competition, I have argued myself that far too many experiments are conducted without a conceptual framework to guide them, making it difficult if not impossible to synthesize meaningful

generalizations (e.g. Keddy, 1989). Meta-analysis is sometimes offered as one way to pull generality out of such experiments, but trying to extract strong generalities (or principles) from a set of experiments that are chaotic and biased seems to be expecting a statistical technique to make up for our lack of planning—and to a large extent it cannot. If there are, for example, no experiments from extreme environments or unusual plant communities, no meta-analysis of studies from temperate zone anthropogenic grasslands ('old fields') will tell us much about wetlands, alpine plants, or savannas. If we accept that vast theoretical models are of questionable utility, and if we similarly accept that a majority of descriptive and experimental studies are haphazard, biased, or phenomenological, it would be easy to conclude that we are trapped in an either/or dichotomy in which both options are unpalatable.

Dichotomies (particularly, perhaps, unresolvable dichotomies) are seductive. Human brains seem predisposed to recognize them, or construct them where they do not exist—us/them; black/white; good/evil; heaven/hell; rich/poor. One way of escaping such dichotomies is to cease thinking about them, replacing this uncomfortable confusion with decisive rule by a strongman. Mussolini, it is said, may have been destructive to Italy and cruel to his opponents, but at least he made the trains run on time. When scientists are faced with a false dichotomy (e.g. theory versus phenomenology, computer models versus nature study), scientists too have the option of simply siding with one powerful personality. Of course, this is intellectually lazy. Yet human history, and yes, even the history of biology (e.g. Mayr, 1982), shows that far too often one extreme seeks power at the expense of the other, effectively suppressing other points of view. Often, an unexpected third alternative provides escape from the dichotomy, which turns out to have been a false one. The objective of this paper is to show that pragmatic models provide an escape from the apparent dichotomy between descriptive and theoretical research.

PART 2. SIX PRAGMATIC MODELS FOR PLANT DIVERSITY

Introduction

One could argue that a goal of ecology in general, and plant ecology in particular, is to find the few essential measurable properties that best describe plant communities and their environments, and then to document the quantitative relationships among them (Rigler, 1982; Keddy, 1987, 1990b; Shipley, 2000). Measurable properties such as biomass, number of species, and canopy height might come to mind first, but the list could be much longer, including nutrient content, evergreenness, leaf size and photosynthetic pathways. Some of the traits might seem to be properties of species, but there is no reason in principle why these could not be averaged over entire suites of individuals and species for a community value. There is a growing consensus that seed size, canopy height and investment per unit area of leaf are three essential plant traits that might be extended to the community level (Westoby, 1998; Weiher *et al.*, 1999).

One could also extend the list of measurable properties to environmental factors, such as nitrogen and phosphorus availability, fire frequency (or variance in above-ground biomass), flood duration or measures of annual precipitation and temperature.

In the longer run, I see the body of knowledge we call plant ecology as consisting of a short set of quantitative relationships that we have documented among a few key properties. These would be pragmatic (or empirical) relationships constructed from real observations, although undoubtedly supplemented by models that offer explanatory power. From this perspective, however, there is no doubt that the pragmatic relationships come first, while studies of mechanism and theoretical models are the secondary step.

In this paper, I focus on one property, or one dependent variable—the number of species in a community. I then explore a number of other properties, or independent variables, that are thought to control the dependent variable. Thirdly, I focus on six general approaches which, while by no means exhaustive, do illustrate how diversity might be controlled at scales ranging from small patches of vegetation to that of landscapes. In presenting these models, I would like to think that I provide a toolbox that could be refined and improved for a future general set of models for the study of plant diversity. I am enough of a pragmatist to suspect that there will never be one unifying model, but rather a set of models, their application being guided by considerations such as scale and location. In the broader picture, I would hope that students of botany will also consider seeking other pragmatic relationships that might constitute a general structure for the field of plant ecology.

1. Species–area model

Larger areas usually contain more species. It is generally true that the number of species encountered in any survey will increase with the time spent searching or with the area that is explored. Time and area are usually related, in that the more time invested in a search, the more ground is likely to be covered. This relationship between species and area can be quantified as

$$S = cA^z$$

where S is the number of species, A is the area and c and z are constants (Rosenzweig, 1995). This exponential relationship is conveniently turned into a linear one by taking logarithms of both sides

$$\log S = \log c + z \log A$$

in which case the constant ($\log c$) represents the intercept of the line and the slope is given by z . This linear relationship was first quantified more than 100 years earlier using plant species in England (Fig. 2). By 1943, Williams (1943) had compiled a global relationship using no less than 238 sites differing in size and location in one figure. Not unexpectedly, the number of species increased with area, particularly at a scale above 1 km² (Fig. 3). 'The richer floras, temperate and tropical are towards the top and the poorer, desert, subarctic and oceanic floras are lower down' (Williams, 1964, p. 96). Williams (1964) also explores

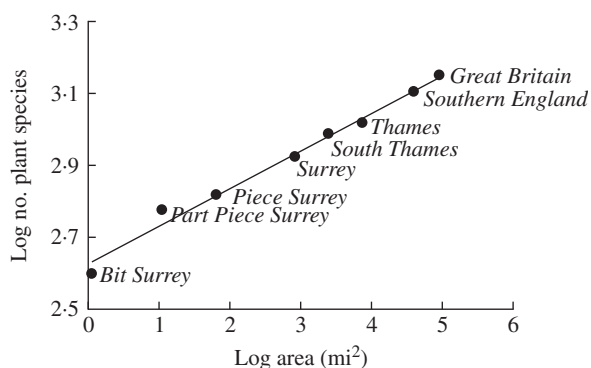


FIG. 2. The first species area curve for the plants of the Surrey region of Great Britain was constructed in 1859 (after Rosenzweig, 1995).

how different processes occur at different scales, and offers some simple models for them (not shown in Fig. 3). At smaller scales, say within a square metre, the number will be influenced by the size of the plants (which will determine the number of individuals that can fit into a quadrat), the amount of competition within and among species, and the degree to which they partition the habitat. Williams observed that this part of the line 'closely follows the relation required by the logarithmic series with a diversity of 10 and one plant per square centimetre' (Williams, 1964, p. 96). On larger scales, the rate of turnover in species composition is likely to become more important, with areas having many endemics, or areas having more variable environments, likely to have higher z values. Other large-scale studies have documented species–area patterns in specific vegetation types, such as Mediterranean-type vegetation (Cowling *et al.*, 1996) and deciduous forests (Silander, 2001). Similar relationships have now been documented for many other kinds of plant and animal species and for many natural areas of landscape (Rosenzweig, 1995). One recent study (Crawley and Harral, 2001) revisited the issue of scale using data from the English flora (while, typically, ignoring Williams's compilation, analysis and hypotheses). In East Berkshire, z is low at small scales ($z = 0.1\text{--}0.2$ at scales $<100\text{ m}^2$), it increases at intermediate scales ($z = 0.4\text{--}0.5$ at scales of 1 ha to 10 km^2), and it then falls back to $0.1\text{--}0.2$ at even larger scales. The underlying reasons are little better understood today than they were when Williams compiled his data.

One of the great values of this model is its immediate applicability to the conservation of biological diversity. The model says quite explicitly that the greater the area of habitat protected in a reserve system, the greater the number of species that will be included. Moreover, it tells us what this relationship is: for every doubling of area there will be an increase of approx. 20 % in the number of species. There is some common-sense logic to this—some species are naturally rare, have very small geographic ranges, or require very specific kinds of unusual habitat, and so will be encountered only if relatively large areas of landscape are explored.

Viewed from the other direction, the species–area model has a depressing reverse logic. As the area of natural landscape decreases (as forests are logged, prairies are ploughed,

wetlands are drained and rangeland is overgrazed), species will disappear with mathematical certainty. Exactly how fast will they disappear? Every time the area of natural habitat is reduced by one-half, the number of species will fall by one-fifth, at least for typical z values. It is sobering to consider just how striking the reduction has already been in many natural ecosystems. As one example, the longleaf pine savannas of the south-eastern United States have lost $>95\%$ of their original geographical area (Christensen, 1988; Platt, 1999). Many natural vegetation types have already been pushed, then, from the upper right to the extreme lower left of Fig. 3.

2. Species–biomass model

Grime (1973a, 1979) observed that habitats with intermediate levels of biomass appeared to have the largest numbers of plant species, at least in British grasslands. He postulated a general unimodal relationship, the 'humped-back' model, between plant-species richness and above-ground biomass (Fig. 4). The suggested mechanism involves two different processes that limit plant diversity at opposite ends of the biomass gradient. Species richness is low at low biomass because of high levels of stress or disturbance, and only a few plant species can tolerate these extremes. Species richness is low at high biomass because of dominance by a few strong competitors that create closed canopies. Ecologists have since tested the model in a variety of habitats including fens (Wheeler and Giller, 1982), lakeshores (Wisheu and Keddy, 1989), interior wetlands (Moore *et al.*, 1989) and Mediterranean grasslands (Puerto *et al.*, 1990). Although there are exceptions to this pattern (e.g. Gough *et al.*, 1994), overall, the 'humped-back' model provides a useful tool for both describing vegetation and, perhaps more importantly, for predicting response to management. Grime's management paper (1973b) can be adapted to most herbaceous vegetation types.

This model works rather well for freshwater wetlands. Figure 5 (top) shows that plant diversity is highest in low biomass sites, although the pattern is strongly skewed to the left, and may be more of an envelope with an upper limit rather than a simple line. If rare species alone are considered (Fig. 5, bottom), the vast majority occur in those sites with very low standing crop ($<400\text{ gm}^{-2}$). For this reason, Moore *et al.* (1989) argue that infertile sites are of particular significance to the conservation of plant diversity. This is likely to become a larger issue with time, as eutrophication from nutrient-laden rain, runoff and ground water increasingly occurs in habitats that were once infertile (e.g. Ehrenfeld, 1983; Ellenberg, 1985; Newman *et al.*, 1996; Keddy, 2000). The presumed mechanism is the increase in biomass with fertility, and the resulting rise in competition intensity, which leads to the replacement of smaller and more-slow growing plant species by tall canopy-forming dominants. In both European grassland and North American wetlands, small rosette species [for typical genera see the centrifugal organization model (no. 3)] are particularly susceptible to loss with increasing fertility.

Debates about the mechanisms producing the model continue. Some suggest that it is simply an artefact arising

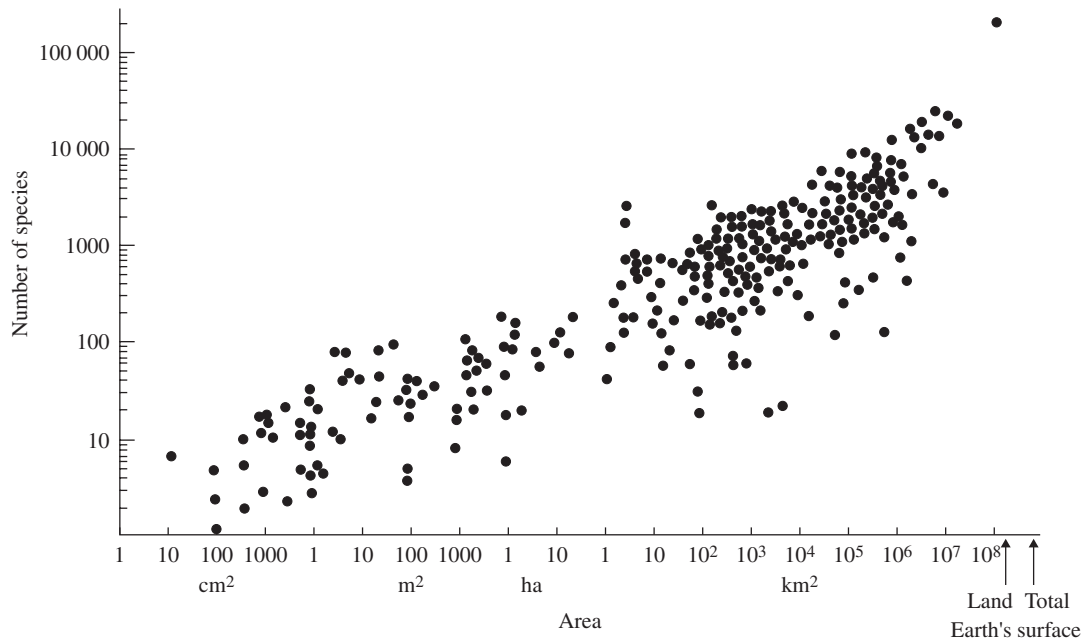


FIG. 3. The number of species of flowering plants found in areas of different sizes at 244 sites (238 from Williams, 1943 plus 6 additional sites in Williams, 1964) around the world (after Williams, 1964).

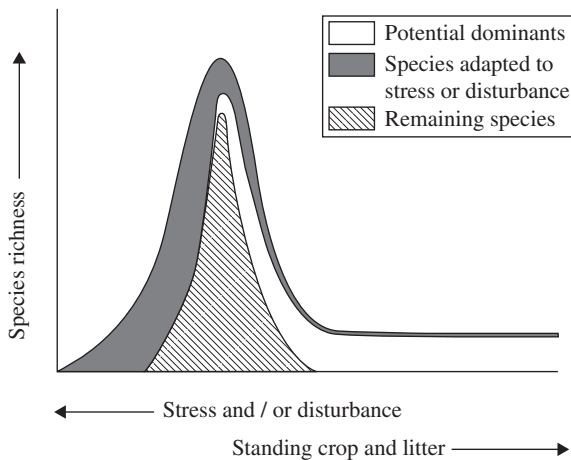


FIG. 4. The species–biomass model (or ‘humped-back’ model) describes the impact of stress and/or disturbance on species richness and species composition (after Grime, 1973a, b, 1979).

from changes in plant size along biomass gradients (Oksanen, 1996, 1997), while others disagree (Grime, 1997; Maranon and Garcia, 1997; Rapson *et al.*, 1997). To some extent, the debate misses the point. Even were this pattern partly a consequence of changing plant sizes, the fact remains that it provides a useful framework for understanding how plant diversity in small patches of vegetation can change with above-ground biomass.

The ‘humped-back’ pattern is scale dependent. It apparently emerges only when one compares different vegetation types. In the classic example, Al-Mufti *et al.* (1977) compared three semi-natural vegetation types—woodlands, grasslands and tall herbs. Each vegetation type provided only one section of the overall relationship. To explore this apparent scale dependence further, Moore and Keddy

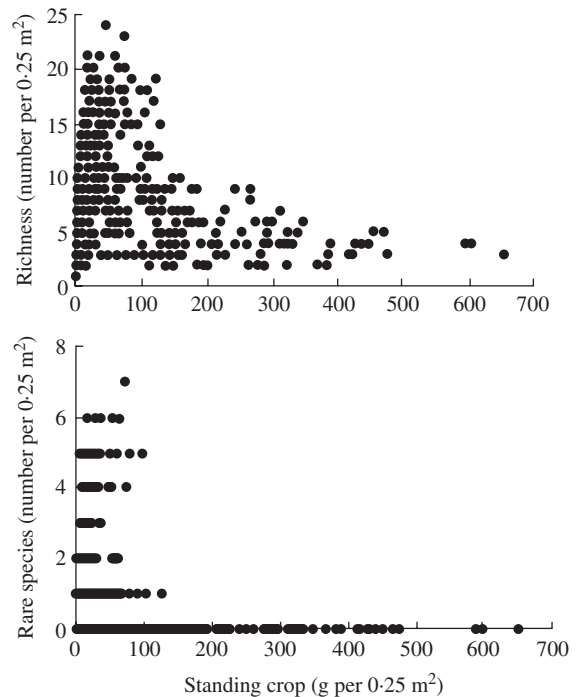


FIG. 5. The species–biomass model for shoreline wetlands based on 401 0.25-m² quadrats from wetlands in Ontario, Quebec, and Nova Scotia (top, all species; bottom, species considered nationally rare in Canada) (from Moore *et al.*, 1989).

(1989) compared species–biomass patterns within and among an array of wetland plant communities. Although the pattern occurred across vegetation types, it did not occur within any one considered alone. Other factors apparently control diversity at these smaller (i.e. within vegetation type) scales.

Future work might consider improved techniques for exploring such patterns. (a) While there is an apparent upper limit to the richness associated with specific levels of biomass, no lower limit is discernible. It may be better to treat explicitly this relationship as an envelope or upper limit (e.g. Scharf *et al.*, 1998; Cade *et al.*, 1999). (b) The predictive power of the species–biomass relationship could be improved by adding additional predictor variables. For example, Shipley *et al.* (1991) included the proportion of species that were functional annuals as a surrogate for disturbance. (c) Structural equation modelling may reveal more details of the complex relationships among soil, biomass, light, and plant diversity (Grace and Pugsek, 1997; Weiher *et al.*, 2004).

3. Centrifugal organization model

In his treatise, du Rietz observes ‘The more different habitats there are in a country, the greater will be the number of species; the more uniform the habitats, the smaller will be the number of species. A plain has not as great a chance of attaining wealth in species as a mountain country’ (du Rietz, 1931, p. 15).

At the landscape scale, we can generalize that the more kinds of gradients, and the greater the range of conditions each represents, the higher the plant diversity will be. One model that can summarize these patterns is called the centrifugal model (Keddy, 1990*b*; Wisheu and Keddy, 1992). The centrifugal model can be thought of as a natural extension of the species–biomass model, but one in which the landscape contains multiple biomass gradients, each controlled by different limiting factors. Imagine a set of such gradients. At one end of each gradient, which we shall call the core habitat, nutrients and water are freely available, which allows a closed canopy to develop and here light becomes a limiting resource. Think, for example, of flood-plains where the core habitat is dominated by *Phragmites* and *Typha*, or old fields with *Solidago* and *Aster* in the core habitat. At the low biomass end of each gradient, however, quite different factors may limit plant growth—say, drought, flooding, high or low pH, low N, low P, or grazing. To tolerate such limiting factors, the plants require different kinds of adaptations, and thus the low biomass end of each gradient supports a different set of plant species. Think of the different kinds of species found in low biomass habitats such as chalk grassland, sea cliffs, alvars, sandy shorelines, rock outcrops, etc. The resulting pattern looks like the spokes of a wheel (Fig. 6), with a set of gradients radiating outward from the core habitat (where light is the main constraint) to peripheral habitats (where a wide array of factors can be limiting). Many unusual genera occur in these peripheral habitats, including *Armeria*, *Asplenium*, *Castilleja*, *Coreopsis*, *Drosera*, *Eriocaulon*, *Isoetes*, *Lobelia*, *Lycopodium*, *Ophioglossum*, *Parnassia*, *Pinguicula*, *Sabatia*, *Saxifraga* and *Utricularia* (e.g. Fernald, 1921–1922, 1935; Peattie, 1922; Soper and Maycock, 1963; Goldsmith, 1973*a*; Moore *et al.*, 1989; Wisheu and Keddy, 1989).

The centrifugal model therefore summarizes the diversity patterns that occur in landscapes containing multiple

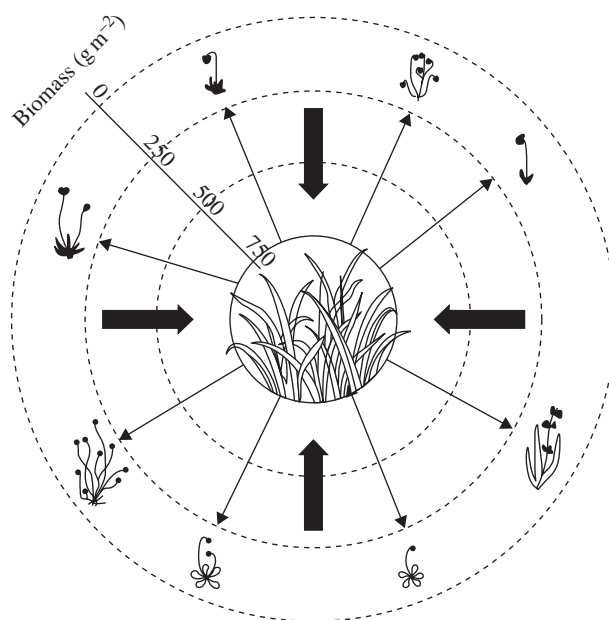


FIG. 6. In the centrifugal model, a set of biomass gradients (thin arrows) radiates outward from one central high biomass habitat. This high biomass habitat, the ‘core’ habitat, is usually dominated by a few large leafy species that are superior competitors for light. The low biomass end of each axis represents a different kind of extreme habitat with one or more strong environmental constraints, and each is often occupied by stress-tolerant species. Many have rosette growth forms (e.g. genera including *Armeria*, *Castilleja*, *Drosera*, *Eriocaulon*, *Isoetes*, *Lobelia*, *Parnassia*, *Pinguicula*, *Sabatia* or *Saxifraga*). Eutrophication causes convergence (thick arrows) in species composition upon a few common nutrient-demanding species.

gradients. Since such landscapes are complicated in structure and composition, they tend to be ignored in more theoretical models that often assume homogeneous habitats. Several predictions arise. First, while the species–biomass model (no. 2) focuses upon a corridor of diversity at intermediate levels of biomass, the centrifugal model emphasizes that over multiple gradients, the lower biomass habitats together are likely to support the largest number of plant species. The larger the number of extreme environments included, the higher the total diversity is likely to be. In terms of reserve design and selection, the centrifugal model draws attention to the need to ensure that extreme and/or unusual kinds of environmental conditions are included. It may be the atypical habitats that contribute most to total plant diversity—rock outcrops (e.g. Wisner *et al.*, 1996; Shure, 1999), alvars (Belcher *et al.*, 1992; Catling and Brownell, 1995), wet meadows (Peattie, 1922; Hill and Keddy, 1992; Sorrie, 1994) or cliffs (Soper and Maycock, 1963; Goldsmith, 1973*a*). Similar types of patterns appear to occur in forests (Keddy and MacLellan, 1990).

The centrifugal model also predicts probable responses to eutrophication. As noted above, eutrophication is a growing threat to plant diversity, as it allows larger canopy-forming plants to exclude smaller stress tolerant plants (Keddy, 2000). Eutrophication will force plant communities that are initially different to converge into one light-limited habitat, thereby leading to even larger losses of plant diversity (Fig. 6, thick arrows)—a growing problem world-wide

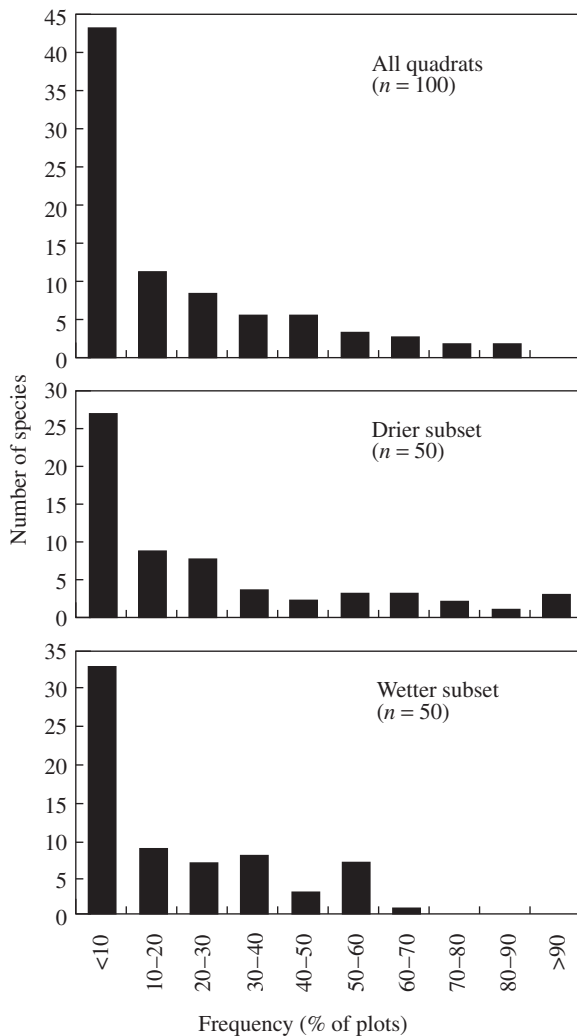


FIG. 7. The relative frequency of plants in wet longleaf pine flatwoods for drier sites ($n = 50$ 1×1 -m quadrats), adjoining wetter sites ($n = 50$ 1×1 -m quadrats), and the two combined. In each case, a majority of the plant species occurred in <10% of the quadrats sampled (courtesy of Meghann Clark).

(e.g. Ehrenfeld, 1983; Ellenberg, 1985; Newman *et al.*, 1996; Keddy, 2000).

4. Species–frequency model

Some plants are more common than others. It has been observed since at least 1909–10 (Raunkiaer, 1909–10) that if one collects data on species presence/absence in a set of quadrats, one tends to find a J-shaped pattern in the distribution of species frequencies. Raunkiaer (1909–10) described this pattern as the ‘law of frequency’. Some data sets show a bimodal pattern, with one large group of relatively infrequent species, and another smaller group of relatively frequent species (Collins and Glenn, 1990; Pärtel *et al.*, 2001). This pattern is by no means universal. Figure 7 shows species frequencies in a set of 100 quadrats sampled in a pine savanna on the Gulf of Mexico coast. At the left end of the axis is a large group

of relatively infrequent species, but there is no evidence of a second group of frequent species. Nearly identical patterns were reported by Kirkman *et al.* (2001). Thus there is not yet even a consensus as to the pattern in such data.

There is a general consensus about patterns found at adjoining scales. At a larger scale, say the total number of individuals in a collection of many species, relative abundance usually follows a log-normal distribution (Preston, 1962a, b; Pielou, 1975; May, 1981). At the other extreme, the very local scale, say the biomass of plants within one small sample, relative abundance usually follows the negative exponential distribution (Whittaker, 1965; Pielou, 1975; May, 1981; Wilson *et al.*, 1996). The species frequency model lies somewhere between these two extremes, and one suspects that all three may reflect an underlying canonical distribution emerging in different manifestations depending upon the style of sampling used. We do not yet know.

Issues of nomenclature may create further problems. If a bimodal distribution emerges (unlike the data in Fig. 7), one can name the two ends of this frequency distribution ‘core’ and ‘satellite’ species (e.g. Collins and Glenn, 1990; Pärtel *et al.*, 2001). The ‘core’ and ‘satellite’ terminology, however, comes from a specific model produced by Hanski (1982). The fact that a pattern observed in the field mimics that produced by a model, does not prove that the assumptions used to construct the model apply in the field. Multiple models can make similar predictions. The two ends of the continuum might also be called ‘matrix’ and ‘interstitial’ species, borrowing from Grubb (1986), but this too assumes certain mechanisms. Terms like fugitive species (Horn and MacArthur, 1972) or peripheral species (Keddy, 1990b) have similar mechanistic implications. Using words like rare and common can also cause confusion, as rarity can occur on many scales (again with poorly known mechanisms; Rabinowitz *et al.*, 1986), and, perhaps more importantly, infrequent species may or may not occur on official lists of rare or threatened species developed by conservation agencies. It seems better to save the word ‘rare’ for this narrower legal and or biogeographic meaning. I suggest that mere observational data be described with terms that do not imply any particular model, mechanism or legal status. Reluctantly, I suggest the use of less colourful, but more neutral language: frequent and infrequent species.

It is remarkable that there is no consensus upon whether bimodality should be expected in this fundamental pattern. Further, there is still no satisfactory mechanistic explanation. We might learn something from the effort invested in the study of relative abundance within quadrats, normally called the study of ranked abundance lists (e.g. Whittaker, 1965; Pielou, 1975). There are many statistical models that might explain differences in relative abundance within quadrats, but no easy way to determine which one is mechanistically correct. Although further progress in documenting patterns found in ranked abundance lists has been made (e.g. Wilson *et al.*, 1996), mechanistic understanding comes from other sources such as field experiments.

Although neither the exact patterns nor their underlying mechanisms are documented, one important generalization still emerges: a majority of the diversity within any one

vegetation type is represented by species that are relatively infrequent. Any superficial inventory of a habitat is likely to over-represent the frequent species. The model also illustrates a fundamental problem in ecological methodology; to test hypotheses and design experiments, adequate sample sizes are required. The frequency distribution tells us, however, that as we include more species, the sample size for each added species is likely to decrease. Moreover, the effort of obtaining adequate sample sizes will increase exponentially with the number of species being included, since adding more species will usually require adding increasingly infrequent species. Most research, therefore, has to be done on common species, with unknown consequences for the field of plant ecology. This could be called the streetlight effect, recalling the story of the drunk who is looking for his keys under the streetlight even though he lost them in an alley. When asked why, he answered that the light was better under the streetlight than in the alley. Since plants are often difficult to identify accurately, except by a small pool of experts, there is a second factor that is likely to further bias our knowledge towards the common species—they are the ones more people can recognize. Since most observers cannot identify the rare plants (particularly in groups like grasses, sedges and asters), it is entirely possible that many studies further underestimate the diversity at the infrequent end of the continuum.

5. Competitive hierarchies model

A few species usually dominate any particular habitat, apparently owing to a better ability to forage for and accumulate contested resources, thereby denying those resources to neighbours (Keddy and Shipley, 1989; Shipley and Keddy, 1994). These species also tend to share a few key traits, usually the ability to preempt light (Keddy and Shipley, 1989; Keddy, 2001). Most of the remaining species in the community (the majority) must survive amidst a matrix provided by these dominant species. Most of the plant diversity in an area therefore consists of weaker competitors. The new challenge is to better document the characteristics of these subordinate species, and how so many of them manage to survive.

Such studies begin with matrices that document pairwise interactions among an entire set of species. Wilson and Keddy (1986) explored pairwise interactions among seven wetland plants and found that the competitive dominant was a canopy-forming sedge, *Dulichium arundinaceum*, while the weaker competitors were evergreen rosette species such as *Eriocaulon septangulare*. The weaker competitors were reduced in abundance, and often entirely restricted to habitats that the canopy-forming species was unable to occupy—open sandy beaches. Gaudet and Keddy (1988, 1995) also showed this pattern in a much larger sample of nearly 50 species. In general, the dominant species occupy fertile and protected sites, whereas the weaker competitors are largely restricted to infertile sandy beaches with recurring disturbance from waves. A similar pattern and mechanism occurs on English sea cliffs; one grass, *Festuca rubra*, seizes the sites with deeper soil and lower salinity, restricting rosette species to the high-salinity, exposed sites

(Goldsmith, 1973a, b, 1978). In dry chalk grassland, the weaker competitors survive in turf so long as low fertility and recurring disturbance reduce the large grasses; fertilization or elimination of grazing lead to dominance by a few grasses such as *Dactylis glomerata* (Grime, 1980). In North American prairies, some plant species avoid competition from prairie grasses by colonizing mounds of fresh soil created by badgers (Platt and Weiss, 1977).

A literature review of pot experiments has verified that dominance by a subset of large and leafy species is a recurring pattern (Keddy and Shipley, 1989), a pattern further confirmed by tests against a null model (Shipley, 1993). The degree of resistance to pragmatic models is shown by the scholarly reaction—this strong combination of data from multiple field experiments using different species, and significance tests of pot experiments against null models had its dissenting voices (cited and responded to in Shipley and Keddy, 1994). Field experiments have shown that when the grasses are removed, other species respond positively and diversity often increases (e.g. Gurevitch and Unnasch, 1989; Brewer, 1998; Jutila and Grace, 2002). These experiments therefore add independent support to the pragmatic model, showing in the field that dominants suppress the rest of the flora.

In this pragmatic model, the larger canopy-forming species form a matrix of biomass (*sensu* Grubb, 1986). Grasses are potential dominants in most herbaceous communities, although the species or genera may differ: *Glyceria* spp. in freshwater wetlands, *Spartina patens* in saline wetlands, *Andropogon* spp. in prairies, *Agropyron* and *Panicum* spp. in wet meadows or *Dactylis glomerata* in limestone grasslands. There are also occasional exceptions, such as the dominance by *Carex*, *Cladium*, *Scirpus*, *Typha* or *Eupatorium* in wetlands (e.g. Keddy, 2000), and the dominance of nettles (*Urtica dioica*) in some fertile upland sites (Al-Mufti *et al.*, 1977). In these cases, however, the dominant plants share a consistent set of traits: tall, dense canopies and a capacity for vegetative spread.

This pragmatic model is largely consistent with the more theoretical view offered for grasslands by Tilman (1982): large canopy-forming grasses tend to dominate quadrats and exclude neighbours. Givnish (1982) has similarly offered a model showing how height confers a competitive advantage in many habitats. Height and shade tolerance are also key factors in many models of forest communities (Shugart *et al.*, 1981; Botkin, 1993). The importance of height is particularly critical when available nutrients and water lead to competition largely for light, and there may be exceptions where below-ground competition predominates (Tilman, 1982; Keddy, 2001).

If the experimental and statistical evidence that plant communities are organized in strong competitive hierarchies is accepted, an important opportunity arises. Instead of asking why a particular species dominates a site, it can be turned around and the opposite question asked: given this strong tendency for competitive dominance, and its apparent linkage with light limitation, how do so many other species manage to survive? When descriptive data and the species–frequency model are examined, it is found that a significant proportion of the species (usually more than half)

occurs at low abundance and frequency. Thus, most of the botanical diversity at a site is in the infrequent species, and it is their survival in spite of competitive dominance that must be understood.

6. Intermediate disturbance model

The final model is actually a class of models that may seem to comprise an unusual mixture, but all share a non-equilibrium perspective on plant diversity. Each, in their own way, answers the problem raised under model no. 5 (competitive hierarchies): given the strong tendency for competitive dominance, and its apparent linkage with light limitation, how do so many other species manage to survive? The answer, in short, is recurring disturbance that removes biomass from the community, and there is a suite of species that exploit such gaps. The significance of disturbance in ecological communities seems to have struck a cohort of ecologists nearly simultaneously in the late 1970s and early 1980s—perhaps an interesting phenomenon for historians—Grubb (1977), Connell (1978), Grime (1979), Huston (1979) White (1979), Pickett (1980) and Sousa (1984). The idea goes back further, e.g. dispersal in patchy environments (Skellam, 1951), ‘the paradox of the plankton’ (Hutchinson, 1961) and ‘fugitive species’ (Horn and MacArthur, 1972).

Disturbance is usually defined rather narrowly, as a factor that removes biomass from a community (Grime, 1979), although in other cases the word is used with broader connotation to include physical disturbances such as animal burrows and erosion (Pickett and White, 1985). Wetlands are notorious as a habitat having vast reserves of buried seeds. We now understand that this testifies to the recurring disturbance that these habitats receive from fluctuating water levels, fire, ice scour and storms (Keddy, 2001).

The intermediate disturbance model (Huston, 1979), nicely summarizes many of these ideas. Diversity is presented as the result of two contradictory forces: rate of disturbance and rate of recovery (which, in turn, determines rates of competitive displacement) (Fig. 8). If the rate of disturbance is altered (say, by altering fire regimes in a landscape), or if the rate of recovery is altered (say, by increased eutrophication), diversity will change. One factor complicating the application of this model is the amount of contingency; the direction of change of diversity will depend upon the present location of the system in two-dimensional space. This prevents simple generalizations about whether a particular event (e.g. increase in fire frequency) will lead to higher or lower plant diversity. Of course, it is this very contingency that increases the realism of the model.

There is an entire set of models that relate to disturbance in small areas. Most, but not all, are used in forests, where gap dynamics are known to have a profound effect on tree species composition (e.g. Shugart *et al.*, 1981; Denslow, 1987; Botkin, 1993). Larger gaps created by landslides (Guariguata, 1990), storms (Seischab and Orwig, 1991), volcanic eruptions (del Moral and Wood, 1993) and flood plain disposition (Salo *et al.*, 1986) can have similar consequences for enhancing diversity in landscapes.

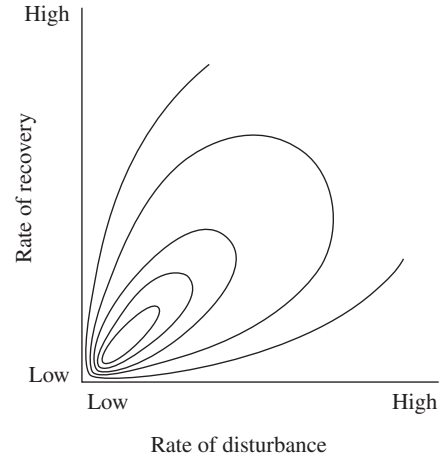


FIG. 8. The number of plant species in a habitat (and the biomass) are a consequence of a dynamic equilibrium between the rate of disturbance and the rate of recovery from disturbance. The inner ellipsoid has the highest number of plant species (after Huston, 1979, in which these axes are designated ‘frequency of [biomass] reduction’ and ‘rate of [competitive] displacement’).

The concept of the species pool

The concept of the species pool (Keddy, 1992; Pärtel *et al.*, 1996; Zobel, 1997) provides a strong conceptual link among at least three types of data: global patterns of plant-species richness (e.g. Williams, 1964; Gaston, 2000; Myers *et al.*, 2000); global patterns of plant evolution (e.g. Takhtajan, 1986); and the species richness of plant communities. It would be valuable to have quantitative and measurable relationships in this realm of inquiry—a seventh pragmatic model. Preliminary explorations have found, for example, that the regional species pool in wetlands is lower at high fertility (Wisheu and Keddy, 1996), that the regional species pool of grasslands increases with pH (Grime, 1979; Pärtel, 2002) and that there is a positive relationship between plant diversity at the local and regional scales (Pärtel *et al.*, 1996). Seeing pools of constant size in a microcosm with different habitat types has shown that very different communities can be assembled from the same pool, depending upon the conditions (Weiher and Keddy, 1995; Vivian-Smith, 1997). For a fixed pool, the number of species in the community decreases with fertility (Weiher and Keddy, 1995) and homogeneity (Vivian-Smith, 1997). Other work includes simple mathematical models for processes affecting pools (Eriksson, 1993). None of these relationships yet has sufficient generality to qualify as a general model distinct from elements already covered in model no. 6.

Several problems must be overcome. (a) The species pool is currently more of a concept (*sensu* Peters, 1980, 1992) than a model—a model must have clearly defined and measurable axes (Peters, 1980, 1992; Keddy, 1987). (b) Generalizations may be limited by the heterogeneity of pools—each pool is a heterogeneous assemblage containing species with different relative abundance, size, evolutionary history, life history traits, growth form and physiology. (c) Quantification is hampered by the practical

difficulty of measuring the number of species in a pool, a difficulty increased by difficulties of terminology (Zobel, 1997; Grace, 2001), particularly when the concept is generalized to animals (e.g. Kelt *et al.*, 1995). (d) There are multiple causal pathways. The regional pool logically sets an upper limit to the local pool, and reduces the size of the pool from which species may be drawn. The pool within each community type, and the number of local communities, will also influence the regional pool. If such problems can be overcome, a future model may link patterns of richness between small and large scales, possibly further unifying the models introduced earlier in this paper.

CONCLUSION

There is a compelling need to protect natural plant communities and to restore them in degraded landscapes. This must proceed guided by sound scientific principles, practical conservation tools and clear priorities. There is also a compelling need for simple effective models that can provide a unifying logical structure for (plant) community ecology. Pragmatic models provide a powerful way of synthesizing existing data, to infer management techniques, and to suggest testable mechanistic hypotheses. I have focused upon six models addressing intermediate levels of heterogeneity, i.e. diversity above the quadrat level and below the biome level, as this is a frequently overlooked class of models, yet the one with great potential to serve conservation and restoration. To advance beyond the work presented here, the following questions could be asked: Are there other models at this scale that I have overlooked? Are there important examples of these models that I have not cited? How can we refine these models to make them more useful to scientists and managers?

In considering this class of models in particular, and the pragmatic approach in general, we do need to consider the degree to which this class of models, and their management consequences, are now either misrepresented or entirely overlooked (e.g. Tilman and Pacala, 1993). This may lead academics and managers alike to overlook pragmatic progress in plant ecology, in which case one can find too many restoration and conservation manuals nearly or entirely lacking in the fundamental principles of plant ecology (e.g. Weller, 1994; Whisenant, 1999). An unfortunate consequence is that too often one finds superb managers who are managing important vegetation types based upon their best instincts and practical experience—yet unaware that their techniques fit into a pre-existing class of models that would allow them to compare and contrast among vegetation types and share information with other managers dealing with different vegetation types. It is not necessary to reinvent models for each of North America's 80+ ecoregions, nor for each of the world's 30+ floristic regions. The task for academics and managers both is to refine these (and other pragmatic models) and adapt them to local circumstances.

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